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ORIGINAL PAPER

Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users

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Abstract

Examining how animals direct social learning during skill acquisition under natural conditions, generates data for examining hypotheses regarding how transmission biases influence cultural change in animal populations. We studied a population of macaques on Koram Island, Thailand, and examined model-based biases during interactions by unskilled individuals with tool-using group members. We first compared the prevalence of interactions (watching, obtaining food, object exploration) and proximity to tool users during interactions, in developing individuals (infants, juveniles) versus mature non-learners (adolescents, adults), to provide evidence that developing individuals are actively seeking information about tool use from social partners. All infants and juveniles, but only 49% of mature individuals carried out interacted with tool users. Macaques predominantly obtained food by scrounging or stealing, suggesting maximizing scrounging opportunities motivates interactions with tool users. However, while interactions by adults was limited to obtaining food, young macaques and particularly infants also watched tool users and explored objects, indicating additional interest in tool use itself. We then ran matrix correlations to identify interaction biases, and what attributes of tool users influenced these. Biases correlated with social affiliation, but macaques also preferentially targeted tool users that potentially increase scrounging and learning opportunities. Results suggest that social structure may constrain social learning, but the motivation to bias interactions towards tool users to maximize feeding opportunities may also socially modulate learning by facilitating close proximity to better tool users, and further interest in tool-use actions and materials, especially during development.

Keywords Social learning strategies · Social learning biases · Behavioral tradition · Cultural transmission · Macaque · Tool use

Introduction

Social learning, in which learning is facilitated by interactions with other individuals or the products of their activities (Heyes 1994), supports the development of biologically relevant skills such as foraging (Galef and Giraldeau 2001; Rapaport and Brown 2008), predator avoidance (Griffin 2004), and mate choice (White 2004) in many animal species. In addition, social learning processes are fundamental to understanding important phenomenon in cultural and biological evolution, such as the distribution of putative traditions in animals (Fragaszy and Perry 2003), why humans are unrivalled in cultural complexity (Dean et al. 2012) and how social learning capacities can promote the biological co-evolution of further cognitive abilities (Tomasello 1999; Whiten and van Schaik 2007). How human and nonhuman animals socially learn has thus been of enduring interest

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to cognitive science, evolutionary biology, ethology, and anthropology.

Recently, cognitive and behavioral research on social learning has expanded from focusing on the psychological mechanisms (e.g., emulation vs. imitation) involved in animal social learning (Hoppitt et al. 2012; Whiten and Ham 1992; Whiten et al. 2004) to understanding how animals make decisions about social learning, such as when, and from whom to socially learn (Barrett et al. 2017; Huber 2012; Kendal et al. 2015; Price et al. 2017; Rendell et al. 2011). These decision rules have also been referred to as learning and transmission biases (Boyd and Richerson 1995; Henrich and Broesch 2011; Henrich and McElreath 2003) or social learning strategies (Laland 2004). Animals may display a wide variety of biases and strategies (Laland 2004; Rendell et al. 2011), which include state-based strategies such as using social information when uncertain, or when one's own behavior is ineffective (Galef 2009), frequency-dependent strategies such as conformism or copying the most common behavior (Whiten and van de Waal 2016). They may also show model-based biases, in which learners' preferences for "who" to learn from are influenced by the attributes of available models such as age (Biro et al. 2003; Dugatkin and Godin 1993) sex (van de Waal et al. 2010), rank (Kendal et al. 2015), prestige (Horner et al. 2010), models' knowledge or skill levels, which possibly lead to increased scrounging payoffs for learners where food-related tasks are involved (Barrett et al. 2017; Coelho et al. 2015; Kendal et al. 2015; Ottoni et al. 2005), as well as learners' social relationships with models, as in the case of kin and familiarity-based preferences (Swaney et al. 2001; Perry 2009). Furthermore, several biases may operate simultaneously, depending on multiple factors such as the availability of models at any given time, environmental contexts, and the types of information being sought (Hoppitt and Laland 2013; Huber 2012; McElreath et al. 2008).

The hypothesized adaptive benefits of learning biases and strategies in allowing animals to minimise potential costs and optimize the efficiency of social learning, have been supported by theoretical models and simulations (Boyd and Richerson 1985; Kendal et al. 2005). In addition, variation in the use of learning biases and strategies, particularly in terms of model-biased learning in animal groups, influences the likelihood that different types of information is propagated socially, with consequences for the distribution and evolvability of behavioral traditions and cultural variants. For example, captive chimpanzees were found to display biases towards adopting the methods of high-ranked individuals when learning a foraging task (Kendal et al. 2015). The authors proposed that in wild chimpanzee populations, a transmission bias towards high-ranked individuals maintains intergroup cultural variation, since low-ranking immigrants would be more likely to adopt the behaviors of higher ranked existing individuals. However, this same bias would hamper the spread of innovations, since in chimpanzees, behavioral innovations are more commonly made by younger, lower ranked individuals [cf. Perry et al. (2017) on innovation in capuchins], and these individuals are less likely to be copied. How social learning is directed within animal groups also influences pathways of social transmission (Coussi-Korbel and Fragaszy 1995). For instance, learning biased towards mothers would result in a predominantly vertical transmission of information, while learning from a larger number of unrelated individuals would facilitate greater oblique or horizontal transmission of information. These potential effects of learning biases on behavioral transmission beg a better understanding of how different animal species utilize various learning strategies. Examples of how these are expressed in the wild are limited, particularly in the context of how young animals acquire skilled behavioral traditions of their social groups (Coelho et al. 2015; Ottoni et al. 2005).

Our study aims to contribute to this endeavor by examining social learning by young individuals in a free-ranging group of long-tailed macaques (*Macaca fascicularis*) with habitual tool-use behavior. Some populations of long-tailed macaques in coastal regions of Thailand and Myanmar use stone tools to percussively extract and consume hard-shelled marine invertebrates and a small variety of plant fruit and seeds. Systematic study of their behavior over the last decade, first at Piak Nam Yai Island in Laem Son National Park, Ranong province, Thailand (Gumert et al. 2009), and more recently, at Koram Island in Khao Sam Roi Yot National Park, Prachuap Khiri Khan province, Thailand (Luncz et al. 2017; Tan 2017), have described the skills and variation involved in macaque tool use. Across the two populations, macaques process at least 56 food species (Gumert and Malaivijitnond 2012; Tan 2016), and vary their techniques and tools according to food properties (Gumert et al. 2009, 2013; Haslam et al. 2013; Tan et al. 2015). Within these techniques, macaques display a variety of 20 action patterns that vary in prevalence between the nine social groups on Piak Nam Yai Island, and between the Piak Nam Yai and Koram Island populations (Tan et al. 2015; Tan 2016). While several action patterns appear typical and common across both populations, others are common only to subsets of individuals, and a few are idiosyncratic behaviors of single individuals. Across the two studied populations, between 76 and 88% of adolescent and adult macaques are tool users while others never acquire the ability.

We have begun to examine the developmental aspects of stone-tool use in macaques through studies on the Koram Island population (Tan 2017). Proficient tool use develops gradually from exploratory manipulation of stones and shellfish beginning in infancy, and evolving over the juvenile period into early adolescence. Prior to around 1.5 years of age, infants' exploratory manipulations consist primarily

of simple actions performed on objects in isolation (e.g., picking up, touching, biting). Between 1.5 and 3.5 years of age, juveniles begin to combine objects more frequently (e.g., rubbing stones on surfaces). Between 2.5 and 3.5 years of age, manipulative episodes appear increasingly goal-directed, resembling ineffective attempts at tool use. Some juveniles begin to more consistently incorporate percussive actions and the requisite objects for tool use (i.e., shellfish, tool stones and/or anvils) into manipulative sequences, but persist through ineffective control of percussive actions, and errors in producing spatial relations and action sequences (e.g., placing a shellfish on top of a tool stone before hitting the stone onto an anvil surface) before their first success. Juvenile macaques, therefore, develop tool-use skills in large part through individual trial-and-error exploration of their physical environments, but these processes are embedded within the larger social context, a phenomenon common to other animals when developing complex tool use (Holzhaider et al. 2010; Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2005; Resende et al. 2008).

Apart from interacting with their physical environments, we have observed that young macaques often maintain close proximity to tool users, and while doing so, watch as they use tools, obtain food scraps from their tool use, and occasionally attempt to touch or take tools and food items being used by tool users. These interactions between young macaques with tool-using group members on Koram Island provides a good opportunity for further examining the social influences and learning biases during tool skill development, and particularly for investigating the model-based learning biases displayed by young macaques as possible social learning strategies. Within their social group, young macaques are exposed to potential tool-using models of different age-sex classes, social attributes, and tool-use characteristics. In addition, the group carries out tool use in an open environment along a relatively flat shore and rarely segregates into discrete foraging parties. This increases the potential for young individuals to interact with all tool-using group members by decreasing environmental constraints on the expression of learning preferences.

In this study, we examined interactions between non-tool users with the tool using group members with two objectives. First, we sought to document and describe these interactions, and test the hypothesis that interactions by juvenile macaques are active efforts to obtain information about tool use from skilled group members. Specifically, we compared how non-tool users at different ages and stages of tool-use development interacted with tool users. We predicted that interactions would be more prevalent in the youngest macaques when tool-use skills are least developed (below 1.5 years of age), than older juveniles in later stages of skill development or early competence (1.5–3.5 years) and macaques that had not acquired tool use past the documented period of development (older than 3.5 years). Furthermore, we predicted that unskilled macaques at different ages would interact differently with tool users, with younger non-tool users displaying behaviors that indicate an effort to observe and learn from conspecifics. We also examined differences between immature and mature non-tool users' preferences for interacting with some tool users over others, by testing whether preferences correlated with tool users' social, demographic, and skill-related characteristics, namely, social affiliation and kinship, age, sex, relative rank, and measures of tool-users' productivity and skill. These analyses contribute simultaneously to our second objective for this study, which is to examine evidence of model-based learning biases, particularly in young macaques' interactions with tool users.

Methods

Study site

Koram Island (N12°14′32″, E100°0′34″) is situated in the Thai Gulf, about 1 km offshore from the mainland in Khao Sam Roi Yot National Park, Prachuap Khiri Khan province, Thailand. The park protects a coastal region on the eastern coast of Thailand, comprising areas of the mainland, islands, and waters of the Gulf of Thailand. The island is arid and contains no freshwater bodies, with limestone karst interiors that are covered with dwarf evergreens and deciduous scrub flora. It is approximately 0.45 km^2 in area with 3.5 km of coastline comprising limestone cliff shore facing the open gulf, and rocky shores and sandy beaches on the coast facing the mainland.

Subjects

We studied one social group of macaques on Koram Island that ranged in group size from 65 to 72 individuals during the study, owing to immigrations, emigrations, disappearances, and new births. A smaller social group of approximately ten individuals also inhabits the island, but are rarely observed and are not included in our study. The group receives food provisioning from tourists that visit the island daily, and as a result, the macaques are habituated and can be observed at close range. We are able to distinguish each individual according to physical appearance. In total, we obtained sufficient data on 68 individuals for inclusion in one or more analyses.

We grouped individuals by age in two ways, according to the two types of analyses carried out during this study. For analyses on age-related differences in interactions with tool users, we divided individuals into three age groups based on age-related changes in tool use skills (Tan 2017). These age groups were infants ($n = 19$; below 1.5 years), juveniles

($n = 14$, 1.5–3.5 years), and adolescent and adult macaques over 3.5 years, collectively referred to as adults for our current purposes ($n = 35$). For analyses investigating influences on young macaques' choices of tool users as interaction targets, we classified macaques either as subjects or targets. Subjects were non-tool users, which we further divided into immature subjects ($n = 27$) below the age group at which tool use is acquired (2.5–3.5 years), and mature subjects ($n = 12$) that had not acquired tool use despite being past the putative developmental period. Targets were tool users aged either 2.5–3.5, 3.5–4.5, 4.5–5.5 years, or older than 5.5 years ($n = 28$).

Data collection and scoring

AT collected data from 17 October 2013 to 2 December 2014, visiting Koram Island daily, weather permitting, for a total of 227 days. From November to January, the region experiences annual monsoon conditions that restrict access to the island due to rough seas, and resulted in fewer days of data collection during these months (5–13 days/month, compared to 20–35 days/month during the non-monsoon season). On average, data collection each day lasted for 4 h around the daily low tide when the macaques are able to forage and use tools in the intertidal zone. The tide cycles that affect Koram Island vary between diurnal and mixed-semidiurnal patterns, in which there is either only one low tide every lunar day, or two low tides of unequal height each lunar day, often with only one low tide receding enough to expose the lower littoral zones where oysters are located.

We utilized a focal sampling protocol in which individuals were followed for 5-min durations according to a randomized order on continuous rotation. As data were being collected as part of a larger study focusing on the ontogeny of tool use skills (Tan 2017), sampling effort on infants was intensified, resulting in a larger number of focal samples obtained for infants (see "Analyses" and "Sampling equivalence"). Each focal sample was recorded on an audio recorder while in the field, then transcribed and scored at the end of each day. During focal samples, we recorded when subjects began and ended foraging, resting, locomotion, and social behavior to establish basic activity budgets. When subjects were foraging, we recorded bouts of interactions initiated by focal subjects with tool-using group members. Duration of interaction bouts with each target, were defined by the time at which behavior was initiated, to the cessation of any interaction behavior for more than 10 s with that target. During each bout, we recorded the types of interaction behavior carried out by the subject (Table 1), whenever possible, we recorded the identity of the target. In some cases, focal individuals obtained the remains of freshly cracked food items in the vicinity of several tool users, making it difficult to determine the target's identity, and we scored target identity as "unknown". Lastly, we scored the distance from the subject to the target during the interaction (within contact distance, i.e., < 1 m, within 3 m proximity, or further than 3 m). If the focal individual entered within 1 m to the target but supplanted the target from the tool use site, we scored "supplant" as the distance category.

When focal subjects were tool users, we further recorded the length of time which they foraged with tools in hand and scored all their tool-use bouts. For each tool use bout, we recorded food type (sessile oyster or motile food item) and the action pattern used (Tan et al. 2015). We scored several characteristics of tool-use bouts that we used as proficiency measures, these were:

1. *Duration* The time taken to crack open a food item, measured by the time between the first and last strike.
2. *Strike efficiency* The number of strikes used to crack open the food item, with fewer strikes being more efficient.
3. *Strike accuracy* The proportion of accurate strikes, out of the total number of strikes used to crack each food item. Accurate strikes were direct impacts by the stone on the food item, and without causing the food item to ricochet from its placement if motile items were being processed. Inaccurate strikes were those that missed the food item or caused it to ricochet from its placement.

Table 1 Behaviors observed during interactions with tool users

Behavior	Description
Watch	Focusing gaze on target from within 3 m for at least 5 s
Obtain food	Retrieving food extracted by the target
Sniff	Places nose near target's face or hands, or food item or tool being held by the target
Reach	Stretching hand towards a food item or tool being held by the target
Touch food	Making contact with a food item being processed, consumed, or held by the target
Touch tool	Making contact with a tool being used or held by the target
Take tool	Takes over possession of a tool being held by the target
Explore tool	Exploring a tool abandoned by the target, for example by sniffing, touching, picking up, and/or manipulating

4. *Tool fidelity* The number of times the focal individual switched tools during each bout of tool use, with fewer switches indicating higher tool fidelity
5. *Success* Marked by whether the subject was able to crack and consume the food item.

In addition to recording and scoring interactions with tool users and tool-use bouts, we also collected social data for determining patterns of social affiliation, and the dominance hierarchy of the group. During focal samples, we recorded the starts and ends of all grooming interactions involving the focal individual, also recording the identities of grooming partners. To infer kin relationships, we used observations of which infants suckled which females since long-tailed macaques do not allo-nurse, and which individuals consistently huddled with and groomed the same juveniles and each other. To determine individuals' relative ranks, we used focal observations of agonistic interactions and their outcomes (i.e., aggression, supplants, and silent-bared-teeth displays of submission), supplemented with ad libitum observations.

Analyses

Age group differences in interactions with tool users

Sampling equivalence

We obtained a total of 6187 focal samples ($M = 89$, SD = 46 samples per individual), across 68 individuals. The number of focal samples obtained, together with demographic information for each subject are provided in the supplementary information (Table S1). We assessed equivalence in sampling times across age classes. A one-way ANOVA showed significant differences in the average number of focal samples obtained per individual [$F_{(2,\ 66)} = 7.23$, $p = 0.001$]. Tukey HSD post-hoc tests indicated that a larger number of focal samples were obtained per infant ($M = 120$, SD = 64), than per juvenile ($M = 70$, SD = 5, $p = 0.004$) and per adult ($M = 80$, SD = 34, $p = 0.004$). Consequently, we accounted for these differences when testing for differences in interactions with tool users across age groups, by incorporating sampling time as an exposure variable in our models (details below).

Regression analyses

We compared across the three age groups (infants: $n = 19$, juveniles: $n = 14$, and adults: $n = 35$) to test our predictions that interactions with tool users change over the development of tool use skills. Specifically, we examined differences in frequencies of overall interactions with tool users, and frequencies of obtaining food, watching tool users, and other interactive behavior not resulting in food acquisition, during interactions with tool users, as well as frequencies of interactions during which subjects were within 1 and 3 m proximity to the target, or supplanted the target.

We modeled each outcome variable as a function of age separately using negative binomial regression models, derived from the classical Poisson regression model traditionally used to model count data. A Poisson distribution is the simplest distribution used for modeling count data such as rates. However, Poisson regression models assume equality between the means and variances of outcome variables, and the likelihood of type I error is increased when the outcome variable is overdispersed, i.e., variance exceeds the mean. Overdispersion can be dealt with using negative binomial models, which include an extra parameter to model overdispersion (Cameron and Travedi 1998; Gardner et al. 1995; Long 1997). We checked for overdispersion in each outcome variable using the function **odTest** from the package **pscl** (Jackman 2008) in **R** (R Development Core Team 2008). The **odTest** function compares the log-likelihood ratios of a negative binomial model to the null hypothesis, which is a regression of a Poisson regression which assumes equal mean and variance, using a X^2 test. Tests revealed overdispersion in all variables except for rate of scrounging during interactions with tool users. In this case, we compared model fits of a negative binomial and Poisson regression according to their Akaike information criteria (AIC) values and selected the negative binomial regression model based on its lower AIC value ($AIC_{\text{negative binomial}} = 477.39$ vs $AIC_{\text{Poisson}} = 966.38$). We therefore, modeled all outcome variables using negative binomial regression models.

We ran each model first with adults as the reference age group to identify differences between infants and juveniles with adults, then with juveniles as the reference age group to identify differences between infants and juveniles. To account for differences in sampling time, and therefore, differences in the likelihood of observing interaction behavior in individuals of different age groups, we incorporated an exposure variable in our models by introducing the logarithm of the number of focal samples as an offset. Models were implemented in **R** using the function **glm.nb()** from the package **MASS** (Venables and Ripley 2002).

Target preferences

Data matrices

Interaction matrix

We built two directed rectangular interaction matrices, one with immature subjects ($n = 27$) on the x-axis and another with mature subjects ($n = 12$) on the x-axis, and with targets

($n = 28$) on the y-axis for both matrices. Cell values represented the percentage of each subjects' interactions with tool users where the subject engaged with each target.

Social relationship matrices

For both immature and mature subjects, we built a grooming-based association matrix, and an association matrix based on inferred kin relationships, to examine how subject's social relationships with targets influenced their target preferences. In the grooming-based association matrix, cell values represent dyadic association indices calculated by dividing the total amount of time that the subject and target spent grooming each other, divided by the summed non-foraging focal time of the subject and target. In the inferred kinship matrix, cell values of 1 are assigned to inferred kin dyads, and cell values of 0 were assigned to non-kin dyads.

Target attributes matrices

We built matrices containing targets' age, sex, and rank relative to subjects, to examine how these target attributes influenced subjects' target preferences. For each attribute, we built two matrices with immature and mature subjects on the rows, corresponding to the two interaction matrices. In these matrices, cell values represent attributes of the target and not the dyad, so the same values are signed throughout each column (Hemelrijk 1990a, b). In the target age matrices, cells contained a 4, 5, 6, or 7, which represented the target's age group from youngest to oldest (age group 4: 2.5–3.5 years, 5: 3.5–4.5 years, 6: 4.5–5.5 years, and 7: > 5.5 years). In the target sex matrices, males were assigned a value of 1, and females were assigned a value of 2. In the relative rank matrices, cells contained a 1 or 0 value, corresponding to whether the target ranked higher or lower than the subject. We based these relative ranks of subjects' dependent rank instead of their basic rank, since juveniles were subordinate to older individuals without maternal support during conflicts.

Targets' tool use characteristics matrices

We built matrices containing (a) targets' rate of tool use (bouts/min), as a measure of target productivity, (b) average strike efficiency, (c) average strike accuracy, (d) average tool fidelity, and (e) proportion of successful bouts. Characteristics (b)–(e) provided proficiency measures since these characteristics were found to improve over tool-use development (Tan 2017). When calculating these characteristics, we included only tool-use bouts carried out on sessile oysters to obtain comparable measures of proficiency across individual tool users. Tool-use characteristics differ between tool-use carried out on sessile oysters or unattached foods since the two food types are processed differently. Not all tool users processed unattached food, and those that did process unattached food more rarely than sessile oysters (Table S1).

Matrix correlations

We first conducted Tau K_r tests for correlations between the interaction matrices with social relationship matrices. Since we were interested in examining whether subjects' target preferences were influenced by target characteristics beyond their social relationships with targets, we conducted further partial Tau K_r tests to control for the effects of grooming and kin relationships on target preferences when significant correlations between the interaction matrix with target attributes and tool-use characteristics matrices were found. Matrix correlations were carried out using the Matrix Tester add-in for Microsoft Excel (Hemelrijk 1990a, b). Probability for all tests was based on 10,000 permutations. Sample size for tests involving immature individuals and tool users was 55, while sample size for tests involving mature non-tool users and tool users was 40.

Results

Age group differences in interactions with tool users

Negative binomial regression analyses revealed differences between age groups in the overall prevalence of interactions with tool users, as well as in the types of interactions carried out with tool users (Table 2), and proximity to tool users during interactions (Table 3).

Prevalence

We recorded 1280 bouts of interactions with tool users carried out by 51 individuals during focal samples ($M = 19$, SD 23, range 0–81 bouts/individual). We recorded interactions with tool users during focal samples for all infant and juvenile subjects, compared to 48% of adults (17 out of 35 individuals). Frequencies of interactions with tool users were higher in both the infant and juvenile age groups compared to adults, with non-significant differences between infants and juveniles.

Types of interactions

Obtaining food from tool users was the most frequently recorded type of interaction across all age groups (Fig. 1a). All individuals that interacted with tool users obtained food, and on average, obtaining food occurred in 92.90% of individuals' interactions with tool users. Infants and juveniles more frequently obtained food from tool users than adults

Table 2 Means and standard deviations of frequencies of total interactions with tool users, obtaining food, watching, and other types of interaction with tool users for each age group derived from our data—infant (In): $n=19$, juveniles (Ju): $n=14$, and adults (Ad): $n=35$

Age/test	Total interactions	Obtain food	Watch	Other
M (SD)				
In	39.74 (27.75)	32.47 (22.97)	9.37 (9.40)	3.37 (5.70)
Ju	25.00 (14.69)	23.50 (13.40)	2.07 (4.18)	0.21 (0.21)
Ad	5.11 (8.63)	5.09 (8.64)	0	0
Model coefficients (SE)				
In Ad	1.82 (0.33)	1.66 (0.34)	25.24 (11220.00)	4.23 (1.06)
Ju Ad	1.76 (0.37)	1.70 (0.38)	24.09 (11320.25)	2.15 (1.21)
In Ju	0.06 (0.40)	−0.05 (0.42)	1.15 (0.46)	2.10 (0.72)
z				
In Ad	5.46**	4.81**	0.002	4.01**
Ju Ad	4.76**	4.47**	0.002	1.78
In Ju	0.15	−0.11	2.51*	2.51*

We controlled for differences in observation times across age groups in negative binomial regression models. Estimated slopes (model coefficients) of the predictor variable, age group, are reported alongside their standard errors. Significant differences between age groups are indicated with * at $p<0.05$, and ** at $p<0.001$, next to the z score for each test. Degrees of freedom for all models was 65

Table 3 Means and standard deviations of frequencies of interactions that were carried out within 1, 3, and >3 m proximity to tool users, and by supplanting tool users, for each age group derived from our data—infant (In): $n=19$, juveniles (Ju): $n=14$, and adults (Ad): $n=35$

Age/test	1 m	3 m	>3 m	Supplant
M (SD)				
In	29.26 (23.99)	1.21 (1.51)	9.47 (6.82)	0.16 (0.50)
Ju	8.93 (10.70)	3.79 (2.99)	8.64 (1.83)	3.29 (3.60)
Ad	1.00 (1.96)	0.49 (0.95)	1.74 (4.43)	1.86 (3.07)
Model coefficients (SE)				
In Ad	3.08 (0.34)	0.91 (0.45)	1.55 (0.37)	−2.78 (0.78)
Ju Ad	2.31 (0.38)	2.19 (0.46)	1.83 (0.37)	0.71 (0.56)
In Ju	0.78 (0.38)	−1.28 (−2.73)	−0.28 (0.38)	−3.50 (0.85)
z				
In Ad	8.95**	2.03*	−7.20**	−7.31**
Ju Ad	6.06**	4.77**	−5.01**	−3.64
In Ju	2.06*	−2.73*	−0.73	−4.10**

We controlled for differences in observation times across age groups in negative binomial regression models. Estimated slopes (model coefficients) of the predictor variable, age group, are reported alongside their standard errors. Significant differences between age groups are indicated with * at $p<0.05$, and ** at $p<0.001$, next to the z score for each test. Degrees of freedom for all models was 65

and did not differ from each other. Adult interactions with tool users comprised solely of obtaining food, and we did not record any occurrences of watching tool users or other behavior not resulting in food acquisition (Fig. 1b, c).

Amongst infants and juveniles, watching tool users was the second most frequently recorded behavior (Fig. 1b vs c). On average, watching tool users occurred in 14.66% of infants' and juveniles' interactions with tool users. Our regression analysis revealed infants watched tool users more frequently than juveniles but did not find differences in frequencies of watching tool users between infants or juveniles with adults to be significant, although we did not record any instances of watching behavior by adult subjects.

Other types of interactions with tool users that did not result in food acquisition were less frequent overall (Fig. 1c vs a, b). On average, infant and juvenile subjects touched tools that were still being used or held by tool users in 3% of their interaction bouts. Sniffing tool user's mouths, reaching for or touching food items being held or consumed by tool users, and exploring tools just relinquished by tool users were recorded in less than 1% of individuals' interaction bouts. Regression analyses revealed that infants more frequently carried out these other types of interactions, compared to both juveniles and adults. Again, juveniles and adults were not found to differ, despite the absence of these interactions by adult subjects.

Proximity to targets

Infants were more frequently within contact distance and within 3 m proximity to tool users than both juveniles and adults. Juveniles were also more likely than adults to be within contact distance or 3 m proximity to tool users. Infants and juveniles also more frequently scrounged from tool users from a distance of more than 3 m than did adults. Adults and juveniles both more frequently supplanted tool users to obtain food than infants. We did not find a significant difference between juveniles and adults in their frequencies of supplanting tool users.

Target preferences

Social relationships

Both immature and mature subjects more often targeted tool users that were closer social associates as measured by grooming-based association indices. Interaction matrices correlated positively grooming-based association matrices (immature: Tau $K_r = 0.27$, $p_r < 0.001$; mature: Tau $K_r = 0.15$, $p_r = 0.01$). In addition, we found a significant correlation between the interaction matrix and inferred kinship matrix for immature subjects (immature: Tau $K_r = 0.29$, $p_r < 0.001$), but not for mature subjects.

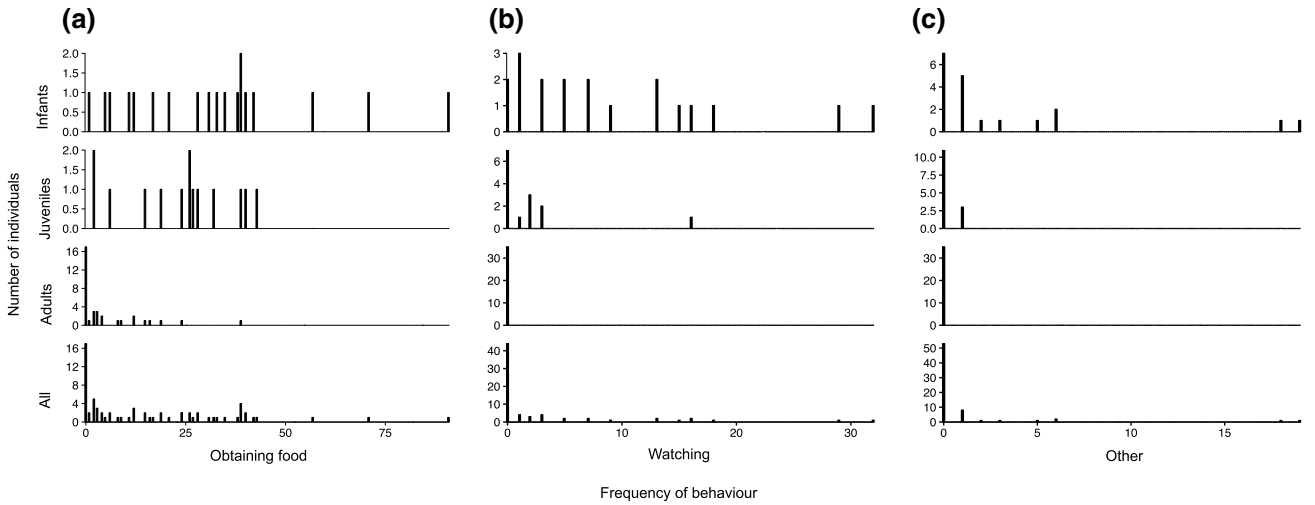

Fig. 1 Frequency distributions of **a** obtaining food, **b** watching tool users, and **c** other interactions not resulting in food acquisition, observed in each age class and across all subjects

Target attributes

Both immature and mature subjects more often targeted female tool users (immature: Tau $K_r = 0.18$, $p_r = 0.02$; mature: Tau $K_r = 0.17$, $p_r = 0.02$). We conducted partial Tau K_r tests to further examine whether this effect was related to sex-differences in tool-use prevalence, or because females as the philopatric sex, had stronger social relationships with targets. The correlation between the interaction and sex matrices continued to be significant when the matrices of tool use rates were partialled out (Immature: partial Tau $K_r = 0.20$, $p_r = 0.01$; Mature: partial Tau $K_r = 0.18$, $p_r = 0.01$). The correlation between the mature subjects' interaction matrix and target sex matrix retained significance when the grooming-based association matrix was partialled out (partial Tau $K_r = 0.14$, $p_r = 0.04$), but not after the inferred kin matrix was partialled out. Preferences for females by immature subjects were no longer significant when either social relationship matrix was accounted for. This result suggests that bias towards female tool users is more likely related to social structure and relationships, particularly for infants and juveniles.

Immature subjects more often targeted older tool users. The interaction matrix correlated positively with the target age matrix (Tau $K_r = 0.17$, $p_r = 0.02$), including when the effects of grooming-based associations (Tau $K_r = 0.15$, $p_r = 0.03$) and inferred kinship (Tau $K_r = 0.19$, $p_r = 0.01$) were controlled for. In contrast, we did not find a significant correlation between target preference and tool user age in mature subjects' interactions with tool users.

On the other hand, tool users' rank correlated with mature subjects' target preferences, but not with immature subjects' preferences. Mature subjects more often targeted lower ranked tool users (Tau $K_r = -0.23$, $p_l = 0.001$).

Tool use characteristics

Interaction matrices for both age groups correlated positively with the matrix containing targets' rates of tool use (immature: Tau $K_r = 0.16$, $p_r = 0.01$; mature: Tau $K_r = 0.19$, $p_r = 0.001$), including when the effects of grooming-based associations (immature: partial Tau $K_r = 0.17$, $p_r = 0.003$; mature: partial Tau $K_r = 0.17$, $p_r < 0.001$) and inferred kinship (immature: partial Tau $K_r = 0.17$, $p_r = 0.01$; partial Tau $K_r = 0.19$, $p_r = 0.001$) were controlled for, indicating that subjects preferred tool users that cracked foods at higher rates and so were more productive.

We also found a relationship between subjects' target preferences and two measures of targets' tool-use proficiency. Subjects preferred targets with higher strike efficiencies on oysters (immature: Tau $K_r = -0.18$, $p_l = 0.004$; mature: Tau $K_r = -0.20$, $p_l < 0.001$), a result that was still significant after controlling for grooming-based associations (immature: partial Tau $K_r = -0.15$, $p_l = 0.01$; mature: partial Tau $K_r = 0.19$, $p_l < 0.001$), and inferred kin relationships (immature: partial Tau $K_r = -0.17$, $p_l = 0.01$; mature: partial Tau $K_r = 0.21$, $p_l < 0.001$). In addition, mature non-tool users also more often scrounged from tool users with a higher proportion of successful tool-use bouts (Tau $K_r = 0.12$, $p_r = 0.03$), a correlation that was also significant when grooming (partial Tau $K_r = 0.12$, $p_r = 0.04$), and inferred kinship (partial Tau $K_r = 0.13$, $p_r = 0.03$) matrices were partialled out. We did not find significant correlations

between the interaction matrix with matrices containing other measures of targets' tool-use proficiency (Table S2).

Discussion

We examined interactions with tool users by different aged macaques at various stages of developing tool-use skills and found evidence to suggest that young macaques are making active efforts to obtain tool use information from skilled group members. We found that all infants and juveniles engaged in interactions with tool users, while only 49% of adult macaques did the same. Furthermore, adult interactions were limited to only obtaining food, and primarily by supplanting the tool user and stealing, or scrounging from a distance. In contrast, young macaques were more frequently in contact distance or close proximity to tool users while scrounging, and also watched tool-users and showed interest in their tool-use actions and tool materials. We further examined how macaques biased their interactions towards available tool users. We found that macaques preferred to interact with tool users with whom they had closer social relationships, and young macaques in particular directed interactions preferentially towards kin. Young macaques preferred older tool users, while mature non-tool users preferentially targeted lower ranked tool users for scrounging. Macaques preferentially interacted with tool users that carried out higher rates of tool use and were more efficient at cracking oysters with fewer strikes. In addition, mature macaques also preferentially targeting tool users with higher proportions of success at tool use. These findings suggest that macaques are preferentially directing interactions at tool users that provide better opportunities for food payoffs, and this may also facilitate better learning opportunities for young macaques (see also Ottoni et al. 2005). We consider various interpretations of our findings and discuss their implications for understanding social learning and behavioral transmission in macaques and other animals. Lastly, we identify avenues for future research that could address the limitations of the current findings, and further contribute towards understanding how animals utilize social learning strategies across varying contexts.

How animals attend to conspecifics' behavior is influenced by the content of interest (e.g., behavioral actions/food/objects), as well as the novelty of information being sought (Huber 2012). In particular, animals may occasionally and briefly attend to group members' behavior if the goal is simply to update existing information. In contrast, when animals seek to obtain new information from group members, as when learning a tool use task, they should attend to group members for longer durations while the behavior of interest is being carried out. The ways in which infant and juvenile macaques in our study interact with tool users show evidence of how animals behave when attempting to acquire new information and indicate interest in the content of tool-using group members' behavior (tool-use actions, stone and food objects) as opposed to merely the end product (potential food).

We found that only infants and juveniles watched tool users at close range for extended durations, suggesting that their visual attention to tool users can be interpreted as observing tool use. In addition, infants compared to juveniles watched tool users more frequently. In contrast, when adults and adolescents looked at tool users, their behavior was momentary (< 5 s and therefore not scored as watching following our ethogram), and usually followed immediately by supplanting the tool user to steal food. Supplanting the tool user interrupts tool use, making it unlikely that adult non-tool users are obtaining information about tool use actions through these interactions. Apart from differences in observation, young individuals also maintained closer proximity to tool users, and directed interactions towards tool-use actions and stones used by group members, for example touching stones being used by targets and exploring used stones. Such interactions involving close proximity and "co-action", have been demonstrated to be important for the learning of techniques in capuchins (Fragaszy and Visalberghi 2004) and captive chimpanzees (Horner et al. 2010), and could also support social learning for young macaques during the development of tool-use skills.

Social learning can be optimized if learners bias their interactions towards group members that can provide more or higher quality learning opportunities. Our results indicate that macaques, particularly young individuals, display affiliative and kin-based interaction biases, and we also found possible payoff-biased preferences for interacting with tool users across all ages. Young macaques in our study showed a strong preference for interacting with tool users with whom they had stronger grooming associations, and who were kin. Familiarity and kin biases have several hypothesized advantages for social learning. It has been suggested that genetic similarities between relatives can increase the probability that related individuals react to experiences and information more similarly, and therefore, increase the likelihood of learning when associating with and attending to kin versus non-kin (Boyd and Richerson 1985; Laland 2004; Price et al. 2017). It is also proposed that psychological biases towards learning from parents could have been selected for since offspring themselves are indications of their parents' reproductive success, and so learning from one's parents could be strategic particularly if the learnt behavior confers reproductive success (McElreath and Strimling 2008).

On the other hand, social learning along kin and social relationships may also arise because of social constraints on learning and may not always be an advantageous strategy. In contrast to our findings for instance, two studies

examining young capuchins' preferences for observing tool using group members when learning how to crack nuts did not find significant associations between social proximity and observation preferences (Coelho et al. 2015; Ottoni et al. 2005), a difference that could be related to species-typical social systems. Capuchin societies are described as highly socially tolerant with food sharing commonly occurring with unrelated adults outside of parent–offspring contexts (Fragaszy et al. 2004), compared to more nepotistic long-tailed macaque societies (Aureli et al. 1997; Matsumura 1999; Thierry 1985). Young macaques may, therefore be interacting more with close associates and kin in tool use foraging contexts simply because these individuals are more likely to tolerate their close proximity and scrounging. This would have implications for learning at the individual level, and for the distribution of tool use within macaque groups. Tolerance is important for learning as it facilitates close spatial proximity between learners and models and allows learners to attend to models' behavior with less interruptions or fear of retaliation (Coussi-Korbel and Fragaszy 1995; van Schaik et al. 2003). Young individuals with a larger number of or more proficient tool-using kin may benefit from being able to preferentially interact with kin, but learning would be inhibited for young individuals without tool using kin or less proficient kin if their interactions were socially constrained in this way. As we have noted previously, not all macaques acquire tool-use skills, and this current finding suggests that social constraints on learning could be a contributing factor.

Additional findings however, suggest that patterns of interactions with tool users are not entirely socially constrained, and macaques can bias interactions towards tool users in accordance with their goals. Obtaining food from tool users was the most common type of behavior displayed during interactions regardless of age, suggesting that the possibility of feeding on otherwise inaccessible food is the primary motivator behind interacting with tool users. Macaques preferentially targeted tool users that carried out higher rates of tool use, and tool users who were more proficient after social relationships were statistically accounted for. These findings demonstrate model-based biases, that may be strategies for maximizing feeding and learning opportunities.

Animals are hypothesized to use model-based strategies for several reasons. Animals may be using heuristic information, such as group members' age and rank, to guide their interactions towards the most successful individuals (Laland 2004). Young macaques in our study did bias interactions towards older individuals, suggesting that this is one possible mechanism. Since tool use proficiency and success increases with age (Tan 2017), preferentially attending to older tool users could simultaneously increase scrounging payoffs, provide better opportunities for observing, and higher quality information about tool use. We did not find evidence that young macaques were biasing their interactions according to tool users' rank. Mature macaques' preferences correlated with rank but were biased towards lower rather than higher ranked individuals. This suggests that mature macaques utilized rank not as a proxy for tool users' skill, but to increase their ability to steal food from tool users.

Model-based biases can also provide indirect indications of various payoff-biased learning strategies, in which animals are capable of evaluating, and basing their decisions of who and what to copy, on the benefits of their own and others' behavior (Boyd and Richerson 1985; Kendal et al. 2009a, b; Vale et al. 2017). Currently, it is unclear if macaques are able to evaluate the outcomes of group members' tool-use behavior. One finding that may indicate this possibility is that the mature non-tool users biased their interactions towards tool users with higher proportions of tool-use success, while young macaques did not. This suggests that mature individuals could be more knowledgeable of the relative proficiencies of tool users than young macaques, an ability that can result from associative conditioning processes (Dawson Erika et al. 2013). In this case, mature macaques' preferences for more successful tool users may result from accumulated experiences with relative payoffs from interacting with different group members.

Regardless of the underlying cognitive mechanisms, the motivation and ability to bias interactions towards the tool users that can provide the feeding and scrounging opportunities could provide a proximate explanation for how these interactions drive tool-use learning in young macaques. The facilitative effects of scrounging on information acquisition are contested (Giraldeau and Lefebvre 1987; Giraldeau and Beauchamp 1999), but scrounging appears to support learning in at least some species. In an experimental study on social learning in marmosets, opportunities for scrounging improved success rates of social learning to open a closed door to access food (Caldwell and Whiten 2003). These studies highlight how a motivation to obtain food increases subjects' attention to skilled models, and thus improves their ability to gain relevant information and learn to perform the task on their own. If macaques are behaving similarly, then young macaques are drawn to tool users because it is an opportunity for feeding. This initial interest then directs youngsters' attention to observing tool-use actions and exploring tool-use materials, and since we only find these behaviors in youngsters, we conclude these explorative behaviors likely serve a learning function.

In summary, our results demonstrate that young macaques actively seek tool use information from group members during development, and bias their interactions in ways that likely affect how young macaques socially learn about tool use, and how tool use is transmitted in macaque groups. Young macaques display preferences for interacting with tool users that were close social associates

or kin, and in addition, preferentially targeted more productive and proficient tool users. These model-based biases may be strategies to increase feeding and scrounging opportunities, which supports learning by maintaining young macaques' exposure to tool use and facilitating individual exploration.

We have discussed several limitations in distinguishing between the possible psychological mechanisms and social environmental influences that could underlie these apparent strategies. These limitations highlight where future research can be most productive. First, it is difficult to discern the extent to which young macaques' target preferences reflect active decisions, and how tightly these decisions might be constrained by social dynamics. In addition, it is likely that individuals may vary their reliance on different strategies according to their own social circumstances (Kendal et al. 2015; Mesoudi et al. 2016). Follow-up studies can examine individual differences in social learning biases, such as whether offspring of non-tool users or less productive tool users might show stronger preferences towards more productive tool users rather than close social affiliates or kin, which will provide a better sense of the extent to which learners are able to strategically modulate their learning. Second, field experiments will be instrumental in elucidating the cognitive mechanisms underlying our observational findings. For example, by manipulating the payoffs associated with experimentally introduced behavioral variants, we may be better able to determine whether our observed model-based biases reflect how macaques evaluate the payoffs associated with their own and others' behavior (e.g., Barrett et al. 2017; Kendal et al. 2009a, b, 2010; Vale et al. 2017). Finally, longitudinal study (e.g., Matthews 2009; Perry 2009) can also examine how different types of interactions, for example scrounging versus watching, and target preferences and learning biases eventually relate to developmental outcomes and inter-individual variation in tool-use behavioral patterns within macaque groups. These efforts will further contribute towards understanding the emergence of social learning biases in animal groups, and their consequences for the maintenance and evolution of animal traditions.

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Research in the Kingdom of Thailand and in Khao Sam Roi Yot National Park was permitted by the National Research Council of Thailand (NRCT), and the Department of National Parks, Wildlife, and Plant Conservation. Research protocols were approved by the Nanyang Technological University (NTU) Institutional Animal Care and Use Committee (ARF SBS/NIE-A 0210 AZ). This study does not contain any studies with human participants performed by any of the authors.

References

Aureli F, Das M, Hans C (1997) Differential kinship effect on reconciliation in three species of macaques. J Comp Psych 111:91–99

Barrett BJ, McElreath RL, Perry SE (2017) Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. Proc R Soc B Biol Sci 284:20170358

Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T (2003) Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Anim Cogn 6:213–223

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press, Chicago

Boyd R, Richerson PJ (1995) Why culture is common but cultural evolution is rare. In: Paper presented at the Joint Royal Society/British Academy symposium on evolution of social behaviour patterns in primates and man

Caldwell CA, Whiten A (2003) Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. Anim Behav 65:1085–1092

Cameron SC, Travedi PK (1998) Regression analysis of countdata. Econometric society monographs no. 30. Cambridge University Press, Cambridge

Coelho CG, Falótico T, Izar P, Mannu M, Resende BD, Siqueira JO, Ottoni EB (2015) Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus spp.*). Anim Cogn 18:911–919

Coussi-Korbel S, Fragaszy DM (1995) On the relation between social dynamics and social learning. Anim Behav 50:1441–1453

Dawson Erika H, Avarguès-Weber A, Chittka L, Leadbeater E (2013) Learning by observation emerges from simple associations in an insect model. Curr Biol 23:727–730

Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN (2012) Identification of the social and cognitive processes underlying human cumulative culture. Science 335:1114

Dugatkin LA, Godin J-GJ (1993) Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. Behav Ecol 4:289–292

Fragaszy D, Perry S (2003) The biology of traditions: models and evidence. Cambridge University Press, Cambridge

Fragaszy D, Visalberhi E (2004) Socially biased learning in monkeys. Anim Learn Beh 32(1):24–35

Fragaszy D, Visalberghi E, Fedigan L (2004) The complete capuchin: the biology of the genus *Cebus*. Cambridge University Press, Cambridge

Galef BG (2009) Strategies for social learning: testing predictions from formal theory. Adv Study Behav 39:117–151
Galef BG, Giraldeau L-A (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 61:3–15
Gardner W, Mlvey EP, Shaw EC (1995) Regression analyses of counts and rates: Poisson, overdispersed Poisson, and negative binomial models. Psychol Bull 118:392–404
Giraldeau L-A, Beauchamp G (1999) Food exploitation: searching for the optimal joining policy. Trends Ecol Evol 14(3):102–106
Giraldeau L-A, Lefebvre L (1987) Scrounging prevents cultural transmission of food-finding behaviour in pigeons. Anim Behav 35:387–394
Griffin AS (2004) Social learning about predators: a review and prospectus. Anim Learn Behav 32:131–140. https://doi.org/10.3758/BF03196014
Gumert MD, Malaivijitnond S (2012) Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am J Phys Anthropol 149:447–457
Gumert MD, Kluck M, Malaivijitnond S (2009) The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman sea region of Thailand. Am J Primatol 71:594–608
Gumert MD, Hamada Y, Malaivijitnond S (2013) Human activity negatively affects stone tool-using Burmese long-tailed macaques *Macaca fascicularis aurea* in Laem Son National Park, Thailand. Oryx 47:535–543
Haslam M, Gumert MD, Biro D, Carvalho S, Malaivijitnond S (2013) Use-wear patterns on wild macaque stone tools reveal their behavioural history. PLOS One 8:e72872
Hemelrijk CK (1990a) A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. J Theor Biol 143:405–420
Hemelrijk CK (1990b) Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Anim Behav 39:1013–1029
Henrich J, Broesch J (2011) On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. Phil Trans R Soc B Biol Sci 366:1139
Henrich J, McElreath R (2003) The evolution of cultural evolution. Evol Anthropol 12:123–135
Heyes CM (1994) Social learning in animals: categories and mechanisms. Bio Rev 69:207–231
Holzhaider J, Hunt G, Gray R (2010) The development of pandanus tool manufacture in wild New Caledonian crows. Behaviour 147:553–586
Hoppitt W, Laland KN (2013) Social learning: an introduction to mechanisms, methods and models. Princeton University Press, Princeton
Hoppitt W, Samson J, Laland KN, Thornton A (2012) Identification of learning mechanisms in a wild meerkat population. PLoS One 7:e42044
Horner V, Proctor D, Bonnie KE, Whiten A, de Waal FBM (2010) Prestige affects cultural learning in chimpanzees. PLoS one 5:e10625
Huber L (2012) What, whom, and how: selectivity in social learning. In: de Waal FBM, Ferrari PF (eds) The primate mind: built to connect with other minds. Harvard University Press, Cambridge, pp 65–80
Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). J Comp Psych 111:159–173
Kendal RL, Coolen I, van Bergen Y, Laland KN (2005) Trade-offs in the adaptive use of social and asocial learning. Adv Study Behav 35:333–379
Kendal J, Giraldeau L-A, Laland K (2009a) The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission. J Theo Biol 260(2):210–219
Kendal RL, Kendal JR, Hoppitt W, Laland KN (2009b) Identifying social learning in animal populations: a new "option-bias" method. PLoS One 4:e6541
Kendal RL, Custance DM, Kendal JR, Vale G, Stoinki TS, Rakotomalala NL, Rasaminmanana H (2010) Evidence for social learning in wild lemurs (*Lemur catta*). Learn Behav 38:220–234
Kendal R, Hopper LM, Whiten A, Brosnan SF, Lambeth SP, Schapiro SJ, Hoppitt W (2015) Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. Evol Hum Behav 36:65–72
Laland KN (2004) Social learning strategies. Anim Learn Behav 32:4–14
Long JS (1997) Regression models for categorical and limited dependent variables. Sage Publications, California
Lonsdorf EV (2005) Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania. Anim Behav 70:673–683
Luncz LV, Tan A, Haslam M, Kulik L, Proffitt T, Malaivijitnond S, Gumert M (2017) Resource depletion through primate stone technology. eLife 6:e23647
Matsumura S (1999) The evolution of "egalitarian" and "despotic" social systems among macaques. Primates 40:23–31
Matthews L (2009) Intragroup behavioral variation in white-fronted capuchin monkeys (*Cebus albifrons*): mixed evidence for social learning inferred from new and established analytical methods. Behaviour 146:295–324
McElreath R, Strimling P (2008) When natural selection favors imitation of parents. Curr Anthropol 49:307–316
McElreath R, Bell AV, Efferson C, Lubell M, Richerson PJ, Waring T (2008) Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. Phil Trans R Soc B Biol Sci 363:3515–3528
Mesoudi A, Chang L, Dall SRX, Thornton A (2016) The evolution of individual and cultural variation in social learning. Trends Ecol Evol 31:215–225
Ottoni EB, de Resende BD, Izar P (2005) Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Anim Cogn 8:215–219
Perry S (2009) Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capuchinus*). Anim Cogn 12:705–716
Perry SE, Barrett BJ, Godoy I (2017) Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. Proc Nat Acad Sci 114(30):7806–7813
Price EE, Wood LA, Whiten A (2017) Adaptive cultural transmission biases in children and nonhuman primates. Infant Behav Dev 48:45–53
R Development Core Team (2008) R: a language environment for statistical computing. R Foundation for Statistical Computing, Vienna
Rapaport LG, Brown GR (2008) Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. Evol Anthropol 17:189–201
Rendell L, Fogarty L, Hoppitt WJE, Morgan TJH, Webster MM, Laland KN (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. Trends Cog Sci 15:68–76
Resende BD, Ottoni EB, Fragaszy DM (2008) Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception–action perspective. Dev Sci 11:828–840

Swaney W, Kendal J, Capon H, Brown C, Laland KN (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. Anim Behav 62:591–598

Tan AWY (2016) Behavioral processes and social influences on the development of stone-tool use in long-tailed macaques. PhD Dissertation. Nanyang Technological University

Tan AWY (2017) From play to proficiency: the ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception–action perspective. J Comp Psych 131:89–114

Tan AWY, Tan SH, Vyas D, Malaivijitnond S, Gumert MD (2015) There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. PLoS One 10:e0124733

Thierry B (1985) Patterns of agonistic interactions in three species of macaque (*Macaca mulatta, M fascicularis, M tonkeana*). Aggress Behav 11:223–233

Tomasello M (1999) The human adaptation for culture. Annu Rev Anthropol 28:509–529

Vale GL, Flynn EG, Kendal J, Rawlings B, Hopper LM, Schapiro SJ, Lambeth SP, Kendal RL (2017) Testing differential use of payoff-biased social learning strategies in children and chimpanzees. Proc R Soc B Biol Sci 284:20171751

van Schaik CP et al (2003) Orangutan cultures and the evolution of material culture. Science 299:102–105

van de Waal E, Renevey N, Favre CM, Bshary R (2010) Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc R Soc B Biol Sci 277:2105

Venables WN, Ripley BC (2002) Modern applied statistics with S, 4th edn. Springer, New York

White DJ (2004) Influences of social learning on mate-choice decisions. Anim Learn Behav 32:105–113

Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. Adv Study Behav 21:239–283

Whiten A, van Schaik CP (2007) The evolution of animal 'cultures' and social intelligence. Phil Trans R Soc B Biol Sci 362:603

Whiten A, van de Waal E (2016) Identifying and dissecting conformity in animals in the wild: further analysis of primate data. Anim Behav 122:e1–e4

Whiten A, Horner V, Litchfield CA, Marshall-Pescini S (2004) How do apes ape? Anim Learn Behav 32:36–52